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# BIOLOGICAL BULLETIN

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## NORMAL VERSUS SUBNORMAL DEVELOPMENT IN *PATIRIA MINIATA*. A CAUTION TO LABO- RATORY EMBRYOLOGISTS.

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(TWENTY-SIX FIGURES.)

Years of experience in rearing marine organisms in finger-bowls of sea water have made the present writer somewhat skeptical as to the validity of life histories worked out under these conditions. The average morphologist who is unfamiliar with the modern refinements of experimental physiology or of ecology scarcely realizes how abnormal as the environment of a marine organism is a bowl of stale and stagnant sea water kept at room temperature and in reach of direct sunlight. Such an organism is adjusted in all of its physiology to the open sea with its uniform temperature, its delicately balanced oxygen content and hydrogen-ion concentration, and its opportunities for selecting light and shade of optimum intensities.

In view of these discrepancies between the natural and the artificial environment it would seem remarkable that finger-bowl cultures ever could approximate normal development. Some organisms, however, are hardy and tolerant of suboptimal conditions and develop in finger-bowls with only slight departures from the normal. Very many marine organisms are, on the other hand, extremely sensitive to suboptimal environmental conditions and show the effects of the finger-bowl environment all too plainly.

A conspicuous example of an organism highly sensitive to suboptimal environmental conditions is the egg of the California starfish, *Patiria miniata*, with which the writer (Newman, '21 a, '21 b) has dealt at some length, calling attention to the numerous anom-

alies exhibited by the larvæ of this species, such as twin gastrulæ and *Bipennariæ* and numerous inhibited types. One would scarcely choose such a species as a favorable object for the study of normal development; yet this very thing has been done by Heath, who in 1917 published an account of the early development of this species.

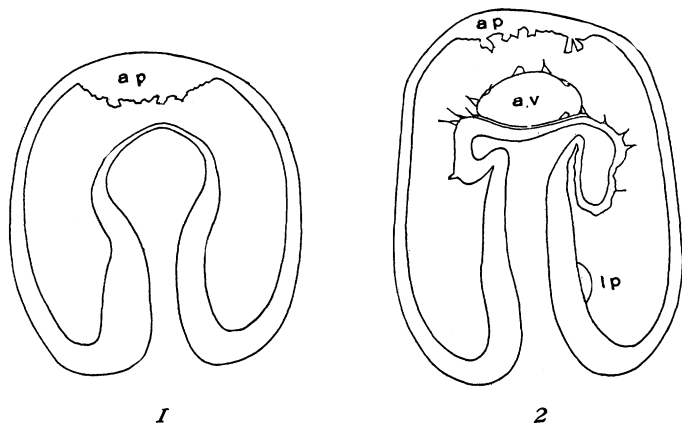


FIG. 1. A gastrula stage, which is obviously subnormal and is to be compared with a normal gastrula such as is shown in FIG. 17. (After Heath.)

FIG. 2. A larva in the stage of cutting off the hydroenterocœl pouches. (After Heath.) *a. p.*, apical plate; *a. v.*, anterior vesicle; *l. p.*, left posterior enterocœle pouch.

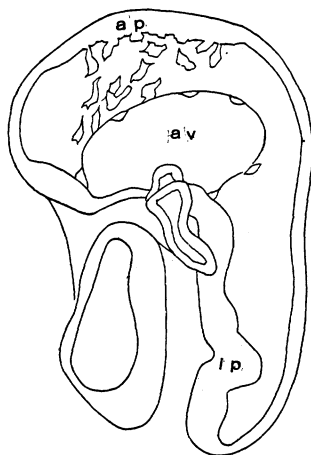
Heath's account was, when it first appeared, very interesting to the present writer because of the rather startling discovery of several characters quite unknown for echinoderm larvæ, but suggestive of enteropneustan conditions. A brief account of Heath's findings must be given in order that the reader may appreciate the present contention.

In the plankton of Monterey Bay a small number of gastrulæ were found which seemed to Heath to combine in a unique way the characters of Echinodermata and of Enteropneusta. Various starfishes were artificially fertilized and reared far enough to show that the first captured plankton specimens were larvæ of *Patiria miniata*.

The artificially fertilized material was reared in finger-bowls and it was found that "the segmentation and early blastula stages do not exhibit any noteworthy features, but beyond this point certain structures arise that have no known counterpart among starfishes. The first of these unique organs is the *apical plate*. In the blastula

stage the cells about the animal pole commence to elongate and, in the gastrula, form a thickened area, more or less lens-shaped in form, having approximately one half the diameter of the transverse axis of the embryo. As indicated in the drawings (Figs. 1, 2), its center is exactly opposite to the blastopore and therefore is strictly apical." Heath notes later that "all of the cells of the apical plate are packed with granules, evidently yolk."

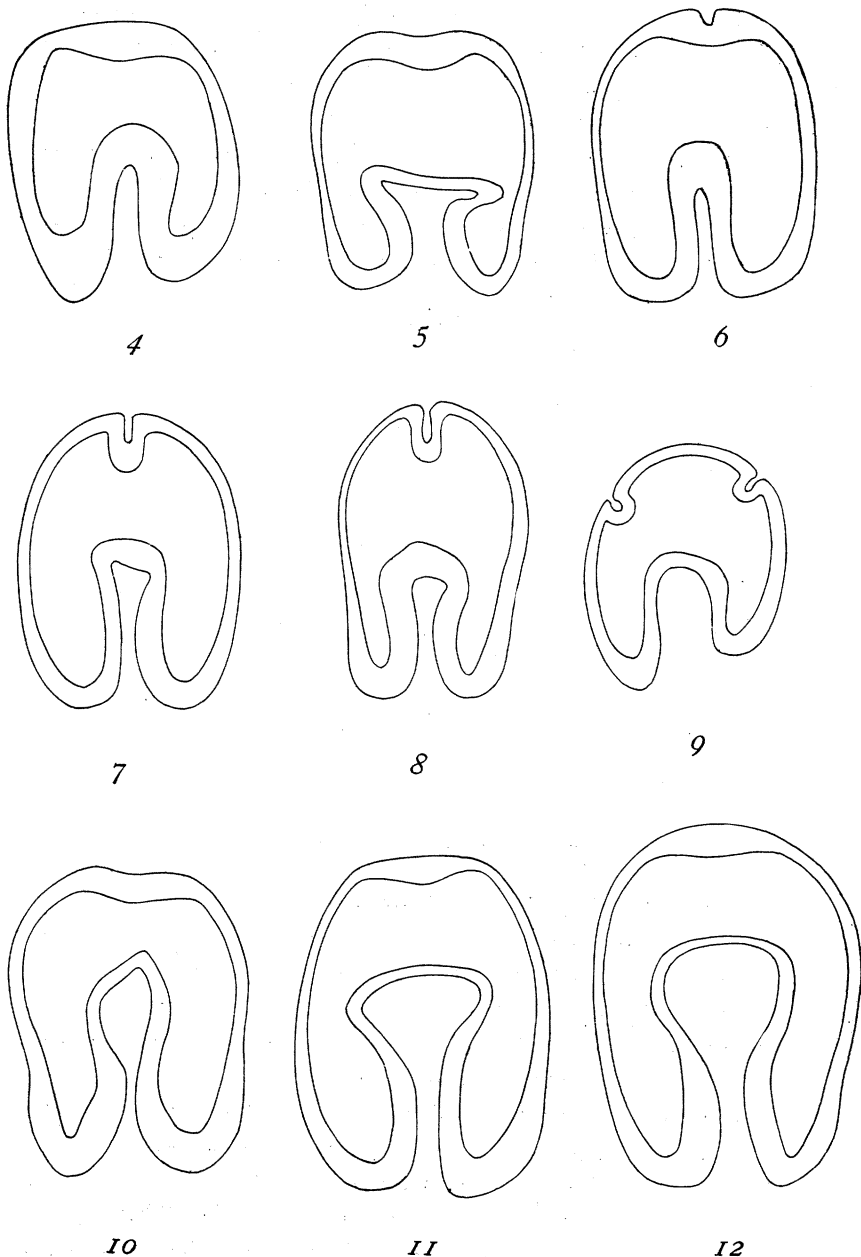
That Heath was entirely incorrect in his interpretation of the structure called by him the "apical plate" is easily shown. The



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FIG. 3. A young *Bipennaria*; a.p., "apical plate"; a.v., "anterior vesicle"; l.p., left posterior enterocœl. (After Heath.)

fact that the cells of this structure are packed with yolk granules should have given him a clue to the real condition; for yolk granules belong to the vegetal pole, not to the animal or apical pole. What Heath saw and accurately described were almost certainly subnormal or inhibited larvæ resulting from parthenogenetic eggs or from eggs inhibited by poor environmental conditions. These never develop normally, but always lag behind and exhibit various anomalous structures. Figures 4-12, inclusive, are camera drawings of a typical series of gastrulæ derived from parthenogenetic eggs of *Patiria*, reared by the writer in finger-bowls in the Pacific Grove Laboratory. These larvæ are all of the same age, about two days old, and are comparable with Heath's first figure (Fig.

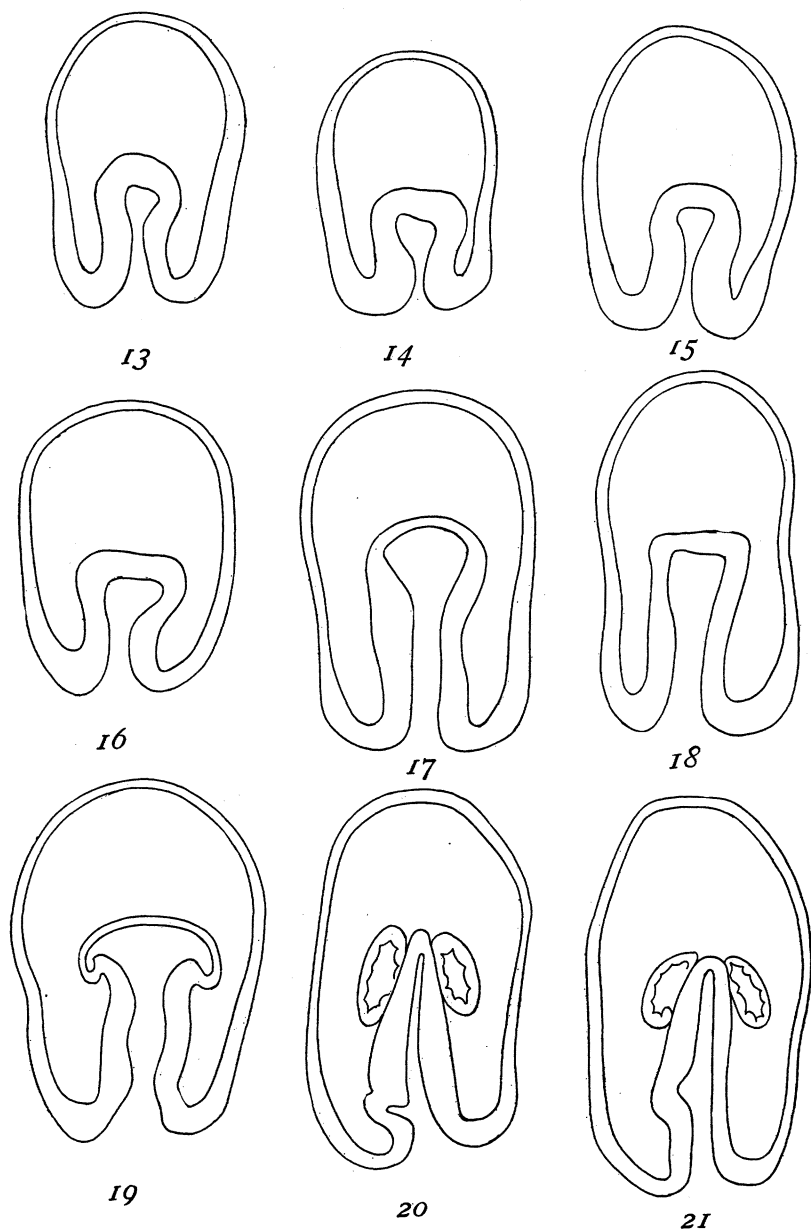


FIGS. 4-12. Camera lucida outlines of optical sections of a series of *subnormal* larvæ derived by spontaneous parthenogenesis from eggs of *Patiria miniata*. In these larvæ the ectoderm in the region opposite the blastopore is frequently thickened and also very frequently invaginates to form secondary archentera. These thickenings do not occur in normal larvæ as may be seen by comparing these figures with Figs. 13-21.

1). It will be noted that the so-called "apical plate" is shown in various forms, ranging from only a slight thickening to a small secondary invagination or even several invaginations. Figure 9 shows one larva with two small secondary archentera. The physiological interpretation of this process of twinning has been given in another paper and does not especially concern us here. Sufficient to say that the so-called "apical plate" is merely a secondary region of low metabolic activity or a secondary area of primitive endoderm, as is evidenced by the presence of yolk granules, and that such a region very frequently invaginates and forms an additional archenteron.

In the light of Heath's descriptions the above sounds like a fairly dogmatic statement and one that should not be made without complete proof. The proof of the above contention is to be found in a study of the truly normal development of the species. If one artificially fertilizes a good ripe lot of *Patiria* eggs, having only a single layer of eggs on the bottom of the dish, uses just enough and not too much sperm, washes out excess sperm and any fragments of ovary or testes after an hour or so, the following conditions will be noticed within about twenty-four hours. A large percentage of gastrulæ like those shown in the camera drawings (Figs. 13 and 14) are found swimming near the surface. These are the normal larvæ and such surface larvæ rarely show any trace of an apical thickening. Near the bottom of the vessel, however, one finds numerous larvæ of the types shown in Figs. 4-9, as well as much more inhibited types. The normal larvæ swimming near the surface are perfectly typical asteroid gastrulæ and are in no way aberrant. If these larvæ are skimmed from the surface and placed in water taken fresh from the open sea, they develop as shown in Figs. 15-23, showing no differences of consequence from larvæ of other asteroids studied side by side with them.

Returning once more to Heath's account, we note that he claims that "in fully 50 per cent. of the specimens in hand a few of the mesenchyme cells arising from the blind end of the archenteron, between the enterocoe pouches, unite to form a small vesicle (Fig. 2, *a*, *v*). This usually occurs after the enterocoe pouches are well differentiated, though not completely cut off." Heath seems to have seen such a thin-walled vesicle quite clearly, if one may judge



FIGS. 13-21. Camera lucida outlines of optical sections of normal larvæ derived from fertilized eggs and drawn off from the surface of the dish. These normal larvæ never show "apical plate" nor "anterior vesicles." FIGS. 13-15 drawn about 24 hours after fertilization. FIGS. 16-18 drawn at about 48 hours. FIG. 19 drawn at 30 hours. FIGS. 20 and 21 drawn at 72 hours.

by his figures. I must admit, however, that in normal material I never could see even the faintest suggestion of such a structure, while in subnormal material I occasionally observed what appeared to be a vesicle of some sort, but even in preserved material it never exhibited anything like complete continuity of outline. Heath describes this so-called "*anterior vesicle*" in great detail, dwelling on its supposed mesenchymal origin and its lack of communication with the archenteron. If, however, such a vesicle is absent in normal larvæ, discussion as to its exact structure loses significance.

A third peculiar structure is described by Heath: "a relatively

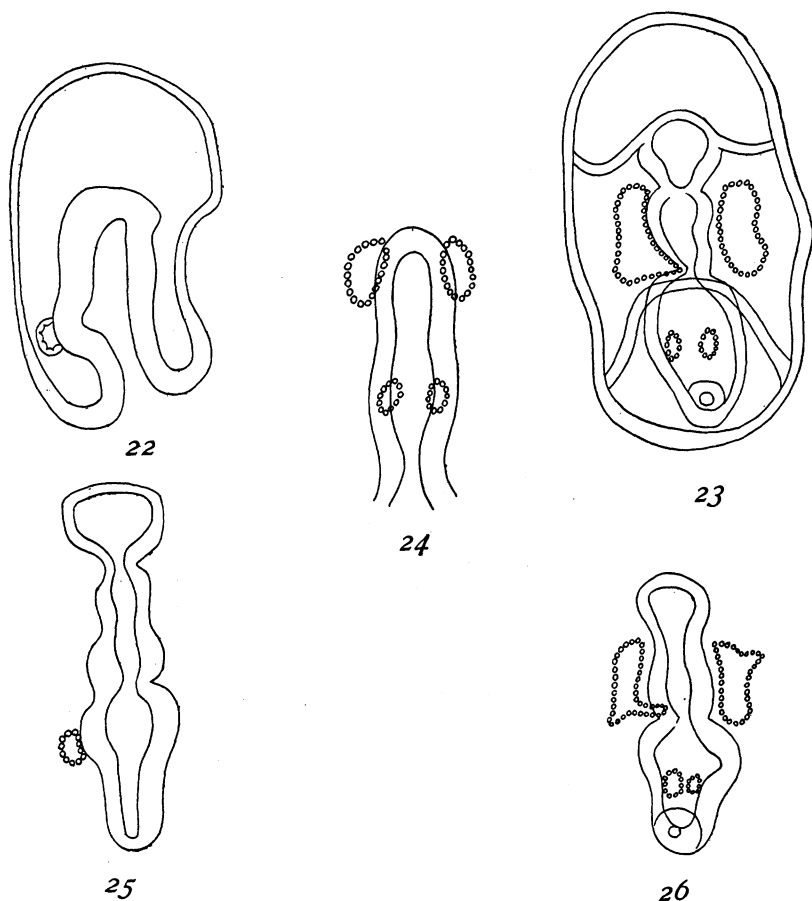


FIG. 22. Right lateral view of larva with single posterior enterocœle vesicle. FIGS. 23, 24, 26 show larvæ with paired posterior enterocœle vesicles. FIG. 25 shows in detail the alimentary tract of a larva with but one posterior enterocœle, on the left.



large vesicle (a posterior enterocœl pouch) present on the left side only." Gemmill had described for *Asterias rubens* a pair of posterior enterocœl pouches which seemed to play little part in the formation of the posterior cœloms, but merely produced mesenchyme. My own observations of the normal *Patiria* larva enable me to confirm Gemmill's findings. More frequently than not two small paired pouches, very thin-walled, appear at about the level of the future stomach. Sometimes only one such pouch appears. The pouch is never large nor thick-walled, as one might infer from Heath's account. The nearest semblance to his structure is seen in my Figs. 20 and 21, where the archenteron shows a unilateral outpouching. Since this condition is relatively rare, however, one can not lay much emphasis upon it. I was not interested in following up the fate of any of these structures, but Heath promises that an attempt will be made to determine their ultimate fate.

On the basis of his observations on *Patiria*, Heath allows himself to engage in rather far-reaching phylogenetic speculations and sums up his position as follows: "I am strongly inclined to look upon the anterior vesicle in *Patiria* as the homologue of the proboscis cœlom of *Balanoglossus*, while the posterior outgrowth corresponds to the trunk cœlom and the intermediate pairs of vesicles in the echinoderms, often with two hydropores in certain species, is the equivalent of the collar cœlom." In another place he says that his discovery of the apical plate in *Patiria* is a strong bit of evidence in favor of the theory that the apical plate of the trochophore larva and of the echinoderm larva are homologous structures. It may readily be seen that to the phylogenist these are speculations of considerable moment, inasmuch as they seem to be confirmatory of the rather current idea that there is more than a superficial resemblance between the Tornaria larva of *Balanoglossus* and the *Bipennaria* and *Auricularia* larvæ of the starfishes and sea-cucumbers.

I have been persuaded to publish this correction of Heath's account merely to avoid the strong probability of the error creeping into our textbooks and becoming part of our permanent literature. Many another error has been thus immortalized; for, once in a textbook, a statement, no matter how erroneous, seems to be passed from generation to generation.

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